Redescription of *Teredicola typica* C. B. Wilson (Crustacea: Copepoda)

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SINCE 1942 *Teredicola typica* has been known to be associated with shipworms in the Hawaiian Islands, but neither the genus nor species has been reported in literature from any other locality, or from any other host group. Dr. C. H. Edmondson of the Bernice P. Bishop Museum, who made the original collections of this interesting copepod, has stated in personal correspondence that he has inquired about the occurrence of copepods in shipworms around the world, but has not yet found anyone who has encountered this parasite. Recently, another copepod parasite has been discovered in *Teredo petiti* from "lagoons of western Africa" by Rancurel (1954). This copepod, for which a new genus *Teredophilus* has been proposed, does not seem on the basis of the description to bear any close relationship to *Teredicola* (see Discussion).

The original description of *Teredicola typica* was made by Dr. Charles B. Wilson in a posthumous paper (1942) and was repeated without emendation in 1944. Records of occurrence of the copepod in the Hawaiian Islands, and observations on its habits and early development are given in papers by Edmondson (1942, 1945). Some corrections and additions to the original description have been made by M. S. Wilson and Illg (1955) in a paper outlining the history and interpretations of the family Clausiidae to which *Teredicola* is referred. The purpose of the present paper is to place on record a revised and amplified description with illustrations of all the appendages, some of which were omitted or confused in the original description.

The specimens examined were from collections of *Teredo milleri* made in Honolulu harbor, January 10, 1945, by Dr. C. H. Edmondson. I wish to acknowledge Dr. Edmondson's cooperation in this study.

Teredicola typica C. B. Wilson, new description
Figs. 1–19

Teredicola typica C. B. Wilson, 1942: 60, fig. 1 a–h; 1944:539, pl. 31, figs. 172–179.
Teredicola typica, Edmondson, 1942:145, fig. 13; 1945:220, figs. 1–3.
Teredicola typica, M. S. Wilson and Illg, 1955: 132.

Length (of specimens examined), female, 4.0–4.71 mm.; male, 1.76–2.21 mm.

FEMALE (Fig. 1). Metasome of four expanded segments; urosome of five posterior segments reduced in width to about one-third of that of last metasome segment. Metasome segments usually swollen and fleshy, dorsally rounded, constricted laterally between segments; integument thin to relatively heavy. Somite of leg 1 united with cephalic segment to form metasome segment 1 (Fig. 2); shape of segment variable, ranging from that with sloped outer margin (Fig. 1) to that with distinct, rounded, distal expansions (Fig. 2).

Urosome segment 1 of female (somite of leg 5) the shortest, marginally free or entirely recessed into last expanded segment of metasome and not visible dorsally; no remnants

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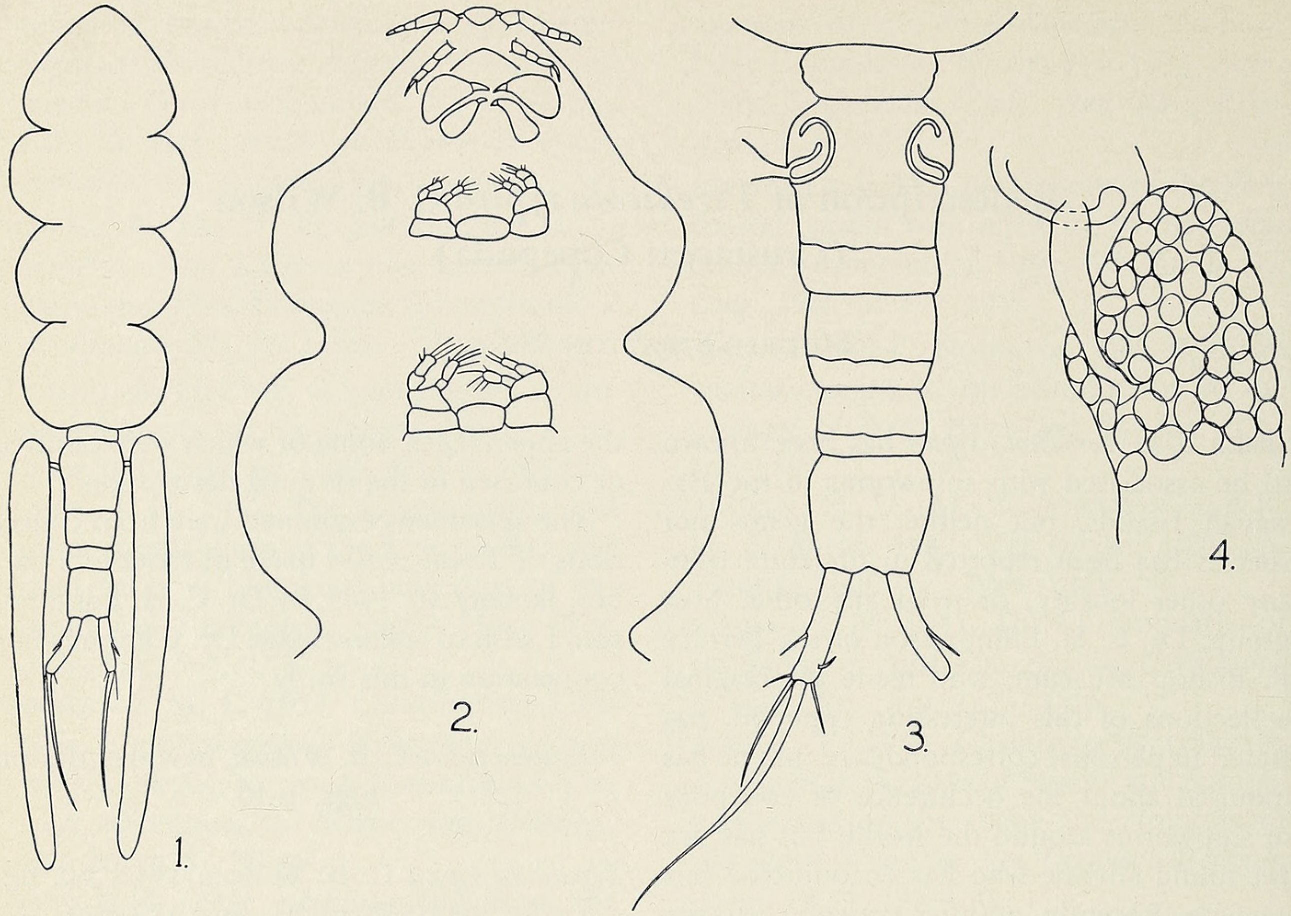
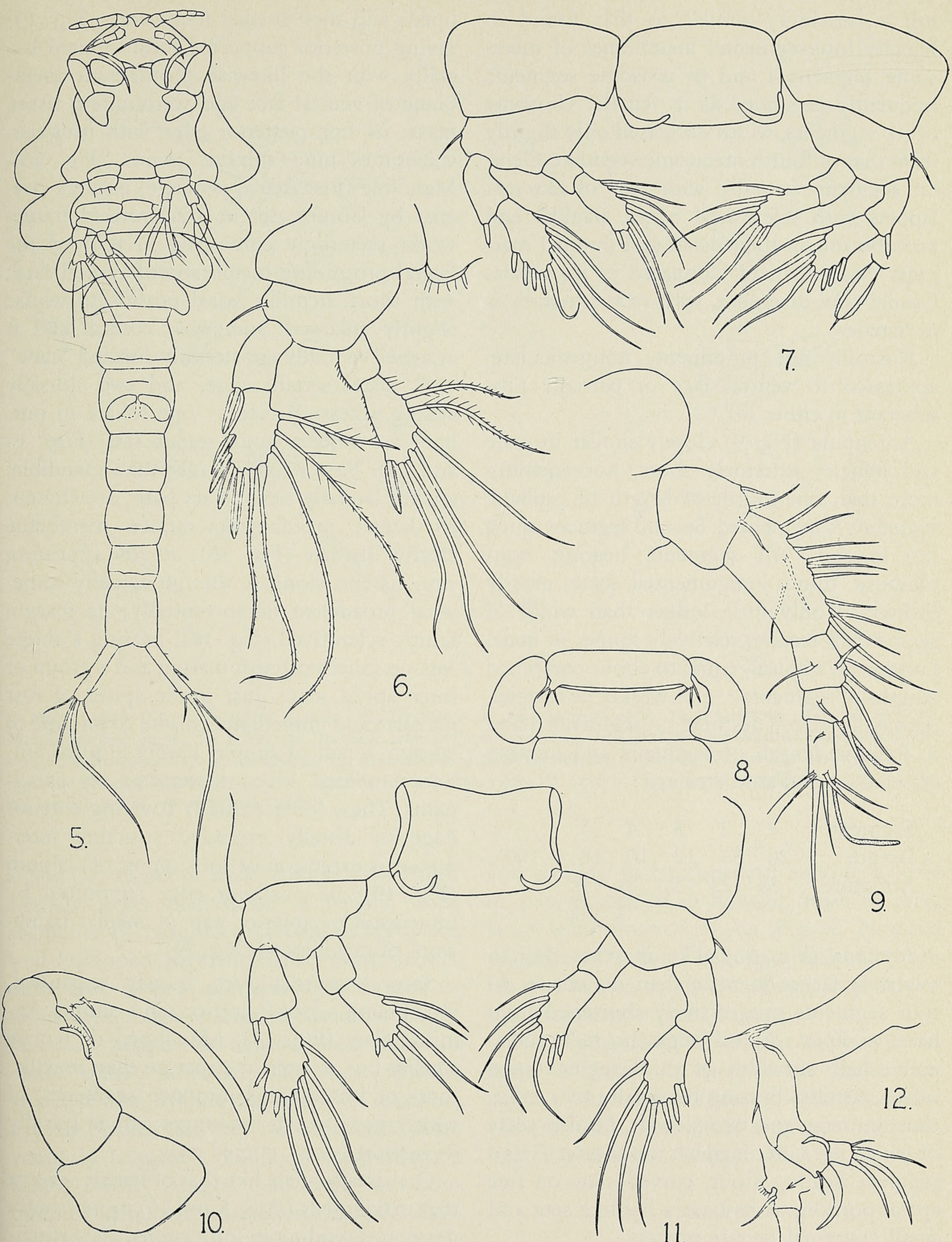


FIGS. 1–4. *Teredicola typica*, female. 1, Habitus, dorsal. 2, Metasome segments 1–2, ventral, showing placement of cephalic appendages and legs 1–2 (same scale as male, Fig. 5). 3, Urosome, dorsal (including thoracic somite 5). 4, Detail of attachment of ovisac.

of leg 5 present. Integument of urosome relatively thin; usually the segments entirely expanded, leaving their broad intersegmental membranes clearly defined both ventrally and dorsally (this shown by wavy line in Fig. 3). Genital segment (urosome segment 2) the longest, proximal portion with slightly rounded lateral expansions. Genital openings dorso-lateral in position, reinforced by strong external sclerotized framework on dorsum (Fig. 3). Ovisacs attached to opening by long, expandable membrane so that the cylindrical sacs are held away from body in "floating" position (Figs. 1 and 4). Sacs reaching beyond caudal rami, attaining length equal to that of metasome or more; with numerous, very small eggs (Fig. 4).

Last urosome segment of female (anal segment) longer than either of two preceding segments and subequal in length to caudal rami; proximal part widened. Rami more or less divergent, slender, length about 4 times greatest width; armed outwardly with short seta placed just below middle and terminally with four setae, the third from outside much stouter and longer than others, its length about 2.5 times that of ramus; small seta placed subapically on inner, dorsal margin.

MALE (Fig. 5). Metasome not swollen as in female but with strongly integumented, laterally expanded dorsal plates broadly curved under ventrally. Lateral expansions of first two segments prominent; those of segments 3 and 4 rather abruptly contracted in width making the division between metasome and urosome less prominent than in female. Fore part of lateral margin of cephalic segment usually gradually and gracefully curved backwards to distal, rounded expansion, but sometimes the whole margin sloped, thus exhibit-



FIGS. 5–12. *Teredicola typica.* 5, Male, habitus, ventral (same scale as female, Fig. 2). 6, Male, leg 1 (same scale as Fig. 7). 7, Female, leg 1, with detail of spine. 8, Male, metasome segment 3, ventral, showing detail rudimentary leg 3. 9, Female, antennule. 10, Male, maxilliped. 11, Female, leg 2. 12, Female, antenna.

ing a variability similar to that found in female. Intersegmental membranes of metasome segment 4 and of urosome segments frequently expanded as in female. Urosome of six segments, width decreased only slightly from that of fourth metasome segment. Genital segment ventrally with pair of external lappets with sclerotized edges, flaplike and protuberant on their distal and internal margins. Anal segment elongated as in female. Caudal rami divergent, with setal armature as in female.

Rostrum not prominent, nongeniculate, appressed to ventral face or partially protuberant in either sex.

Antennule (Fig. 9) closely similar in male and female; extremely short, not equaling more than one-fourth of length of cephalic segment; 5-segmented. Second segment much the longest. All segments bearing nonplumose, thinly integumented setae; mostly shorter or only little longer than width of segment in female, relatively longer in male. Longest seta apical, equal to about combined lengths of segments 3–5. A weakly developed, terminally placed aesthete on segments 4 and 5. Relative length of segments and number of setae (s) and aesthetes (a):

Segment	1	2	3	4	5	
Length	26	38	12	10	14	= 100
Armature	3s	12s	5s	2s	7s	
				a	a	

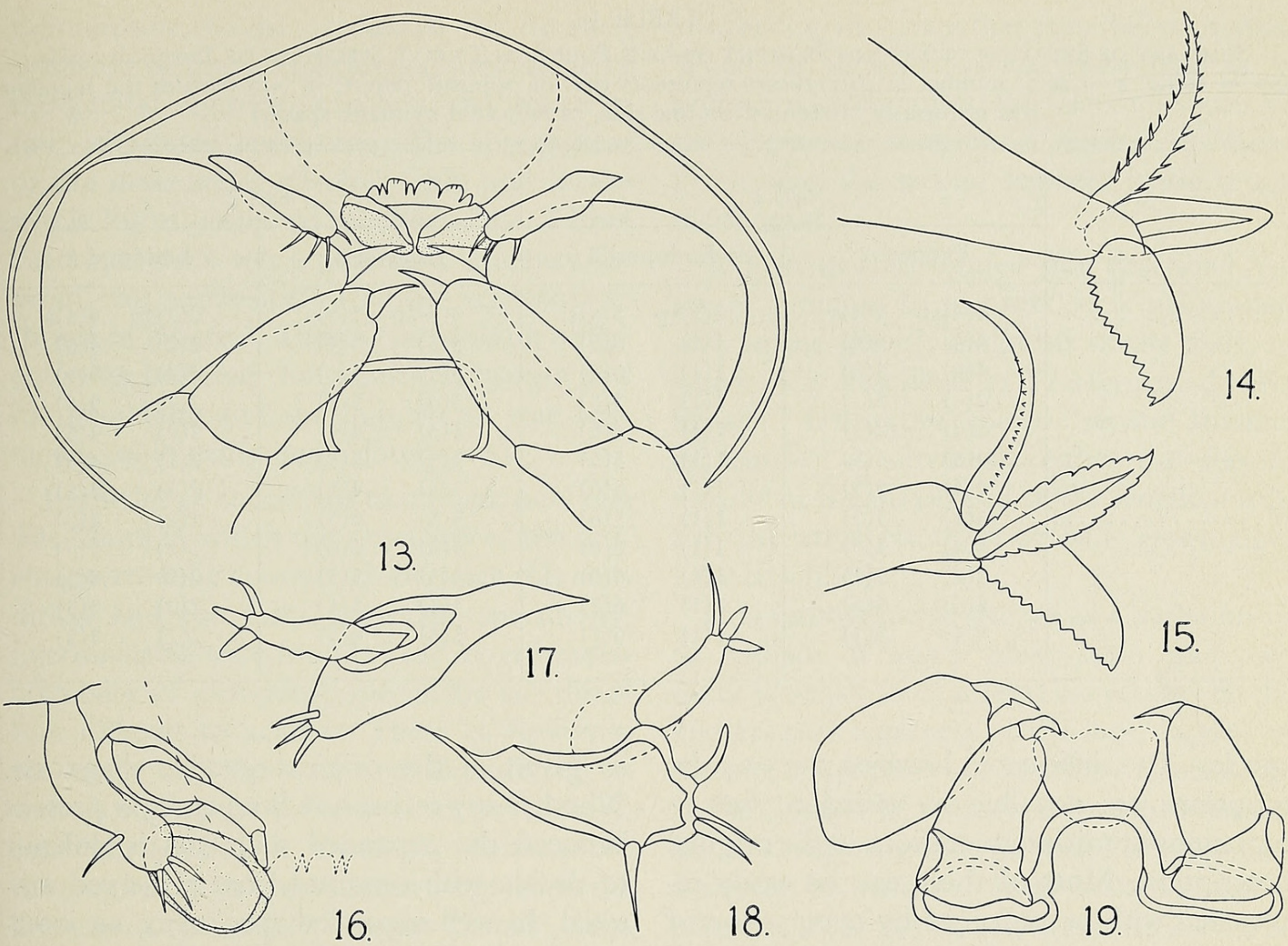
Antenna (Fig. 12) alike in sexes though relatively larger in male than in female, its four segments progressively shortened from base to apex. Apical segment reduced to about half of width of third segment and offset laterally, bearing terminally two stout, clawlike setae and two slender, flexible setae of which the outer is much the shorter. Third segment bearing stout, curved claw on free apical portion; at its base a hairlike seta and small, marginal, serrate process.

Buccal mass outwardly protuberant from ventral face; labrum and its extensive framework forming anterior medial support, maxillipeds and their medial framework (Fig. 19) giving posterior support. Labrum united laterally with the likewise protuberant membrane of ventral face and surrounding tissue mass; its free posterior edge with irregular, sometimes bifid spinous points (Fig. 13). Mandible (first free appendage) entirely covered by labrum, set in a sclerotized framework, seemingly embedded in fold of the lateral protruding membrane of ventral face; with short, stemlike basal portion to whose slightly enlarged, somewhat conical end is attached ventrally a posteriorly directed "claw" with distal serrate edge, and two dorsally arising accessory pieces—one foliate in outline, the other a stout, serrate seta (Figs. 14 and 15). First maxilla larger than mandible, arising laterally beyond its base; attachment to lateral protuberant surface membrane clearly distinct (Fig. 16); *in situ* appearing sinuous and elongate though actually somewhat broadened dorso-ventrally; its margin faintly sclerotized (Fig. 18); bearing a single seta on inner posterior margin and a group of three apical setae. Just inside apices of first maxillae and immediately distad to midline of labrum, a pair of simple, hardly protuberant, unornamented lobes interpreted as paragnaths. These lobes partially covering anterior edge of distally extended structure interpreted as extension of (or support of) labium (Fig. 19); its posterior edge supported by protrusion of anterior part of medial framework of maxillipeds (Fig. 19).

Second maxilla with hugely expanded, membranous basal portion and simple terminal claw (Fig. 13). Maxilliped of female smaller but stouter in structure than maxilla, more or less divided into two segments, of which the second is the longer; armed apically with short, stout, curved claw.

Oral area of male like that of female, except that maxillipeds (Figs. 5 and 10) more stoutly developed, ending in long curved claw reaching back to basal origin of appendage.

Only two pairs of legs present in both sexes (legs 1, 2), much reduced in size (Figs.



FIGS. 13–19. *Teredicola typica*, female. 13, Oral area *in situ*, diagrammatic. 14, Mandible apex, ventral. 15, Mandible apex, dorsal. 16, Schematic diagram, latero-ventral view, showing arrangement of labrum (dashed lines), mandible, first maxilla, and paragnath. 17, Mandible and basal framework overlying first maxilla, showing distortion due to cover glass pressure. 18, Same as 17, different view. 19, Second maxilla and maxillipeds with skeletal framework *in situ*, viewed from below.

2 and 5), those of male comparatively and actually larger than those of female. Both segments of basipod and connecting piece well developed; segment 2 usually with slender outer seta, otherwise unarmed. Both rami 2-segmented, much reduced in size, their length less than basipod in female, about same in male. Spines modified; flat, with narrow, faintly serrate, hyaline membrane on margins; usually tipped with free minute point. Setae variously developed, tending to have enlarged bases, mostly longer than segment, non-plumose in female, sparsely so in male. Exopod segment 1 with single outer spine, endopod segment 1 unarmed. Number of spines on second segment of exopod and endopod of both pairs of legs alike in male and female and tending to be constant; varying a little in size, especially in female; those of male larger than those of female (Fig. 6). Number of setae of second segment variable, both from specimen to specimen and from left to right ramus of a pair (Table 1).

No remnants of other legs in female. In male, a group of three setae present on slightly produced portion of widened ventral plate of third metasomal segment, interpretable as rudiments of leg 3 (Fig. 8).

VARIATION

There does not appear to be any question that the different lots of specimens examined by C. B. Wilson and myself represent the same

TABLE 1

SUMMARY OF SETATION OF SECOND SEGMENT OF LEGS FOUND IN TWELVE SPECIMENS OF *Teredicola typica* (sp = spine; s = seta; number in parentheses represents that of opposite ramus; in two females the segment was previously broken off on one side, as indicated by blank space.)

	LEG 1				LEG 2			
	Exopod 2		Endopod 2		Exopod 2		Endopod 2	
♀	4(4)sp	4(4)s	1(1)sp	5(4)s	3(3)sp	5(5)s	2(2)sp	4(3)s
	4(4)	5(4)	1(1)	6(5)	3(3)	5(4)	2(2)	4(5)
	4(4)	5(6)	1(1)	6(5)	3( )	5( )	2(2)	5(5)
	4( )	5( )	1(1)	5(5)	3(3)	5(4)	2(2)	5(5)
	4(4)	2(3)	1(1)	4(5)	3(3)	4(4)	2(2)	4(5)
	4(3)	3(5)	1(1)	5(5)	3(3)	3(4)	2(1)	4(5)
	4(4)	5(5)	1(1)	6(6)	3(3)	4(5)	2(2)	5(5)
♂	4(4)	5(5)	1(1)	5(6)	3(3)	6(5)	2(2)	4(5)
	4(4)	5(5)	1(1)	6(6)	3(3)	6(6)	2(2)	5(5)
	4(4)	5(5)	1(1)	6(6)	3(3)	5(5)	2(2)	5(5)
	4(4)	4(6)	1(1)	6(7)	3(3)	5(5)	2(2)	5(5)
	4(4)	5(5)	1(1)	6(7)	3(3)	4(5)	2(2)	5(5)

species. The differences between the two descriptions are not due to variation, but to omissions or misinterpretations in the original description. Most of these can be easily reconciled with or explained by comparison of the statements and illustrations in Wilson's description, or with the specimens used in this study.

Teredicola typica clearly shows in both sexes the same recognizable number of body segments most commonly found in both free-living and parasitic cyclopoid copepods—that is, nine segments in the female and ten in the male. As is shown both by Wilson's illustration and those given here, the tumid condition of the anterior part of the female's body does not obliterate the number of segments included in the metasome in either dorsal or ventral view. The lateral expansions are constricted between the segments whether the specimen is newly molted or older, expanded or contracted. The somite of leg 1 is thoroughly united with the cephalic segment as indicated in ventral view (Fig. 2), and the three succeeding expansions are obviously interpretable as the somites of legs 2–4, or thoracic segments 2–4. The fourth thoracic segment cannot be the first reduced segment as given in the original generic diagnosis. Whether any real suture lines are ever present between the expanded segments is difficult to decide with certainty from preserved material. In well expanded specimens, an intersegmental membrane was prominent (Fig. 2), and no definable lines of separation were noticed. In less expanded specimens, complete or incomplete lines were observed, of which some at least were "fold" lines of the membrane. Thus, although highly modified, the metasome of *Teredicola typica* does conform in the female to the "standard" segmentation of other cyclopoids and exhibits external evidence of this.

There are five reduced posterior segments (urosome) in the female, rather than six as shown by Wilson. It follows from the division of the metasome that the first of these is the somite of the absent fifth leg (fifth thoracic segment). The second reduced segment is the genital segment, as is clear from the attachment of the ovisacs, which are shown by Wilson attached to an additional segment posterior to the second segment, an error corrected in an illustration by Edmondson (1945). The extra segment of the urosome shown in this position by both Wilson and

Edmondson can be accounted for by their inclusion of the intersegmental membrane of the genital segment, which is very broad in fully expanded specimens. The integument of the urosome is relatively thin and in the whole lot of preserved specimens that I have examined there was a dominant tendency for prominent expansion of all the segments as shown in Figure 3. There is no striking differentiation between the segmental margin and its membrane and the number of true segments could easily be misinterpreted.

In the lot of specimens examined, only one was found in which the segments of the urosome were fully contracted. Between this condition and the fully expanded specimens, intermediates were found. True length measurements of individual specimens are therefore difficult to achieve. There is, however, no doubt that there are considerable real as well as superficial differences in total length between specimens. From my observation, the range of length measurements given in the literature is reasonably accurate (female, from about 4.0–5.0 mm., male, 1.75–2.35 mm.).

Because of the variation found in the shape of the cephalic segment in both sexes, examples of the extremes of these conditions were particularly examined in detail for possible correlated differences in both body and appendages, but none were found.

The caudal rami exhibit many degrees of divergence in both sexes and it seems evident that this divergence results from an extremely flexible attachment rather than from any real individual or sexual variability. No sexual dimorphism was found in the number or relative size of the caudal setae, although as happens in all copepods, they were at times broken. Most of them are very slender and can be observed accurately only at high magnification.

No variation was found in the segmentation of the antennule. Both Wilson's figures and his statement that the basal segment is nonsetiferous, points to his inclusion of the surface eminence to which the antennule is attached, giving six rather than five segments. When his illustrations are interpreted as 5-segmented antennules, the relative lengths of the segments correspond closely to those given here, the second segment being much the longest.

Wilson neither figured nor described the actual antenna. In the text, it is mentioned only in the generic diagnosis of the male, in which it is described as "2-segmented, prehensile." His figure labeled "second antenna of female" is obviously either the second maxilla or the maxilliped of the female, probably the latter. No other cephalic appendages were described.

It is impossible to accept as a variation or to explain Wilson's observation that two outer setae (or short spines) are present on the first exopod segments of the legs, instead of the one spine observed in all my dissections. In the Copepoda, two spines have been found on this segment only in the Platycopiidae, a family far removed from these cyclopoid parasites. It is difficult to accept this even as an anomaly, nor is there present any cuticular spinous production of the segment itself to allow for misinterpretation. Otherwise, Wilson's figures agree fairly well with the legs examined in this study, though neither the asymmetry nor the variation in the number of setae was noted.

The number of spines on the second exopod and endopod segments of the legs appears to follow a pattern, but even this may be disturbed as shown by the female specimen in which one exopod of leg 1 and one endopod of leg 2 had the usual spinal number reduced (Table 1). Asymmetry of setation was the rule in the females dissected, no individual being found with right and left rami alike in both legs. Though two males had both pairs symmetrical, the two specimens did not completely agree with one another. It is evident from these observations that the setal formula can be used for specific differentiation in this genus only upon examination of several specimens.

INTERPRETATION OF ORAL AREA

The highly modified and usually compact oral areas of poecilostome cyclopoids present particularly difficult problems in both the technical and graphical aspects of their study. Doubtless this has contributed to the differing interpretations of their anatomical features and the omission from many descriptions of all or part of the appendages. The viewpoint has already been expressed that "no species or genus should be proposed without thorough delineation of all the appendages" (M. S. Wilson and Illg, 1955). It is, of course, obvious that neither a taxonomy adequate for identification and differentiation of species, nor one that will contribute to classificatory knowledge, can result from neglect of some parts or mere cursory examination of others.

The illustrations presented here for *Teredicola typica* are diagrammatic and their understanding may be helped by further elucidation of some points. As noted in the description, the buccal mass is protuberant. It is supported anteriorly by the labrum and its framework and posteriorly by the maxillipeds and their framework (Fig. 19). An apparently newly molted specimen, relatively nonfleshy and with thin body membranes, was used for Figure 13. It is a camera lucida drawing from an *in toto* preparation, slightly flattened by cover glass pressure, and viewed ventrally with the compound microscope. Its illustration cannot be other than diagrammatic, since the original is of necessity distorted, but such a view does establish the continuing relationship of the parts, which is impossible to show otherwise.

The labrum is strongly united with the likewise laterally protuberant surface membranes, though a lightly sclerotized line appears to define its actual lateral boundaries (shown by dashed lines in Fig. 13). The ventral posterior edge is free and protuberant.

The mandible is entirely hidden in an *in toto* view, both because of its small size and its location below the labrum. It seems to be somewhat separated from the other appendages by a slight fold of the laterally protuberant membrane. As verified from dissection, the base arises from a shallow framework of anastomosed, sclerotized strands, from which it was usually automatically separated during the manipulation of dissection. Because of the extreme reduction in size of the whole appendage, the apical pieces of the right and left mandibles possibly may not meet one another in midline, but this was not exactly determined. They do, however, reach at least to the free posterior edge of the labrum, below which the oral opening is presumably situated. Figure 16 shows schematically the relationship of the mandible, maxilla, and paragnaths to the labrum. The exact placement of the appendages and other structures may perhaps be more easily determined from early copepodid stages in which the buccal mass is probably not so fleshy and protuberant.

In situ, the first maxilla is elongate and appears to lie along the top of the inflated basal part of the second maxilla (Fig. 13). In actuality, its medial portion is slightly expanded dorso-ventrally, and lies close to the likewise expanded top portion of the second maxilla. In dissection, the two maxillae were frequently separated together, entirely free from the mandible.

Since the relationship of the two anterior appendages in poecilostome cyclopoids has been much disputed in literature, some comments on their relationship and structure in *Teredicola* are appropriate here. The stemlike portion of the mandible appears to be attached to its skeletal framework near the apex of the first maxilla. When the whole buccal mass or separated anterior portions of it were observed and manipulated under the stereoscopic microscope in lateral view and from above, it was clear that the mandible is more deeply embedded (that is, more dorsally situated) than any part of the maxilla. This is a normal and expected condition when the protuberant nature of the whole mass is considered. When the two appendages were dissected together with their surrounding tissue mass and viewed laterally, the more dorsal origin of the mandible and the separate insertions of the two appendages were clearly apparent.

Preparations of some of these dissections made for study of detail under high power objectives are particularly instructive as examples of distortion due to cover glass pressure. Figures 17 and 18 are diagrams of two examples of such mounts. In each the anterior appendage (mandible) and a portion of the framework from which it arises, partly overlies or underlies the posterior appendage (first maxilla) and appears to be attached to the latter. The study and illustration of prepared mounts such as these, in which the two appendages lie in a wholly unnatural relationship, have probably been responsible for or have at least contributed to the continuing argument as to whether or not Sars (1918) was correct in interpreting these two appendages as the maxilla and its attached palp. In this instance, however, if there were a real attachment between these two appendages, the condition in *Teredicola* would represent a reversal of the Sarsian interpretation inasmuch as the smaller anterior appendage (the maxilla of Sars) would be attached to the larger posterior appendage (the palp of Sars). The reduced anterior appendage of *Teredicola* corresponds structurally to the main body of the maxilla of Sars by virtue of its modified apical armature. The larger posterior portion corresponds in its simple setal armature to the so-called palp of other poecilostomes. Quite obviously, if the condition shown in Figure 17 were realistic, it would negate the argument that the first free appendage must be called a maxilla because its armature resembles portions of that found in some other copepods.

It may be useful to other workers to include here some personal remarks about the requirements and techniques of study of the oral area of poecilostomes. It seems to me that, in addition to knowing the details of isolated appendages, it is instructive to know their relationship to one another *in situ*, and to the other structures and the framework of the mass. At least schematic drawings of the whole oral area should be included in descriptions of new or little known genera. In species in which the cephalic segment is tumid, as it is in *Teredicola typica*, it is necessary to remove the buccal mass *in toto* from the ventral face, not only for its own study, but for dissection of appendages. Attention is drawn here to the micro-shears designed by C. S. Wilson (1953), because they greatly facilitate work with such fleshy masses.

In poecilostomes with extremely compact, fleshy, or protuberant masses and highly modified appendages, I have found it essential for personal understanding of the relationships of the appendages to the buccal mass and to one another to study unmounted material and to alternate the study between the stereoscopic and compound microscopes. Although it is not possible to secure high enough magnification for study of detail with the stereoscopic microscope, it does give the third dimensional, natural depth that is lacking in views under the compound, and contributes greatly to interpretation.

SYSTEMATIC POSITION

Teredicola has been referred to the family Clausiidae (M. S. Wilson and Illg, 1955) in a revised and restricted definition limiting the family to the genera *Clausia*, *Seridium*, *Mesnilia*, *Teredicola*, and the inadequately known *Rhodinicola*. The close relationship of this family to the Clausidiidae is pointed out, and the intermediate condition of the apical armature of the mandible of *Teredicola* used to suggest that further study may lead to a merging of the two families or establishment of an inclusive, higher category.

It is not necessary to discuss the classification further since the matter has been dealt with in the previous paper. In assigning other species to *Teredicola*, it will probably be found